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LIFE-HISTORY OF THE VERMILION-SPOTTED NEWT (*Diemyctylus viridescens* Raf.)^{1 2}

BY SIMON HENRY GAGE.

THE working out of the complete life-history of this newt has extended from 1819-1820, when Say and Rafinesque first considered it, until the present year (1891). During this period of seventy-two years it has been the subject of numerous investigations; but from the striking changes in coloration, habit, and structure passed through in its various stages of development it has proved unusually puzzling to the naturalist and physiologist. The phases in its life-history are briefly as follows:

1. The ova are laid in water, and give rise to larvæ with well-developed gills. In course of development these larvæ assume the vermilion spots and general viridescent coloration of the adult.

2. The gills are absorbed, the viridescent coloration changes to a yellowish-red of varying brightness, the vermilion spots remain, the oral epithelium changes from a stratified non-ciliated to a ciliated epithelium, and the respiration and life become wholly terrestrial.

3. In from two to three years the newt changes its red for a viridescent coloration, returns to the water, loses its ciliated and regains a stratified non-ciliated oral epithelium, and reassumes a partial aquatic respiration, and during the remainder of its life is properly an aquatic form.

Historical.—In Vol. I. of the *American Journal of Science*, Say ('19, p. 264) under the name of *Salamandra punctata* Gml. gives

¹ Synonymy, modified from Cope ('87, p. 207): *Triturus* (*Diemyctylus*) *viridescens* Raf. ('20), *Triturus* (*Notophthalmus*) *miniatus* Raf. ('20), *Salamandra punctata* Gml. Say ('19, p. 264), *Salamandra dorsalis* Harlan ('27, Vol. VI., p. 101), *Salamandra symmetrica* Harlan ('25, Vol. V., p. 158), *Salamandra millepunctata* Storer ('38, Vol. III., p. 60), *Salamandra greenii* Gray (Griff. A. K., IX. Syn., p. 107), *Salamandra coccinea* DeKay ('42, p. 81), *Triton dorsalis* Holbr. ('42, Vol. V., p. 77), *Triton millepunctatus* DeKay ('42, p. 84), *Notophthalmus viridescens* Baird ('50, p. 264), *Notophthalmus miniatus* Baird ('50, p. 284), *Triton punctatissimus* Dum. Bibr. ('41, p. 154), *Triton symmetricus* Dum. Bibr. ('41, p. 154), *Diemyctylus miniatus* Hallowell ('56, pp. 6-11), Kelley ('78, p. 399), *Triton viridescens* Strauch ('70, p. 50), *Molge viridescens* Boulanger ('82, p. 21).

a very good description of the viridescent form, and near the end adds: "The younger specimens vary considerably in being on many parts of the body destitute of black punctures, and in having the dorsal and ventral color of the same pale orange. It is decidedly aquatic." As the last sentence follows without explanation, it apparently applies to both the young and the old, and is rather confusing.

The year following Rafinesque, in placing several Urodeles in his new genus *Triturus*, remarks with reference to the adult *Diemyctylus*: "It must form a peculiar subgenus *Diemyctylus*"; and with reference to the red form he says: "It has almost the characters of the subgenus *Diemyctylus*, but differs from it by having the toes of the fore feet free and unequal, the lateral ones much shorter, whence it may form another subgenus, *Notophthalmus*." That is, the adult viridescent and the immature red form were by Rafinesque placed in different genera.

This was continued by some authors, as DeKay; by others the two were placed in the same genus, although considered specifically distinct. It thus continued until 1850-'51, when Baird put both in the same genus, and remarks concerning them: "The salamanders were formerly divided into two great genera, *Salamandra* and *Triton*, the former with rounded tail and terrestrial habits, the latter with compressed tail and aquatic. The necessity of further division has, however, become apparent, and the old distinction into land and water salamanders is no longer tenable as parallel to any anatomical features. Thus, of the highly natural genus *Notophthalmus* (*Diemyctylus*) one species (*Diemyctylus viridescens*) is the most aquatic of all American forms, the other (*D. miniatus*) the most terrestrial; yet the

Common Names.—1. Of the adult aquatic form: Spotted salamander, aquatic salamander, many-spotted salamander, common triton, spotted triton, crimson-spotted triton, spotted newt, water newt, eastern water newt, common newt, spotted eft or evet. 2. Of the red form: Scarlet salamander, yellow-bellied salamander, symmetrical salamander, red lizard, little red lizard, rain lizard, red salamander, red newt, red eft or evet.

Distribution.—Representatives of the genus *Diemyctylus* are found in Europe, Asia, and North America. In North America are two well-marked species,—the *D. torosus* of the Pacific slope, and *D. viridescens*, the subject of this paper, throughout a large part of the eastern region. (Cope, '87, p. 202.)

² The numbers in parentheses refer to the bibliography at the end of the paper.

two are so much alike in shape as to render it a matter of some difficulty to distinguish them."

Five years later this close similarity of the red and aquatic forms so clearly enunciated by Baird led Dr. Hallowell ('56) to express the opinion that "*Diemyctylus viridescens* and *D. miniatus* are probably the same, the orange color and roughness being appearances which, the female more especially, presents after a long sojourn on land. At least this may be inferred from the known habits of the European Tritons."

Again, three years later Cope ('59) says: "We include in the above synonyms (of *Diemyctylus viridescens*) those of the nominal species *D. miniatus*, which we think with Dr. Hallowell ('56) is a state of *D. viridescens*. We have caught specimens . . . of every shade of color between vermilion and brownish-green. The color or character of the skin seems to be dependent upon the amount of moisture in the situations in which they are found. Those from high and dry spots are redder and rougher than those from marshy situations. Thus it is probable that this species undergoes changes similar to those of the European Tritons."

During the next twenty years opinions pro and con were expressed by various systematists, but the final and satisfactory proof of the identity of *Diemyctylus viridescens* and *D. miniatus* was given by Dr. Howard Kelly ('78), who "brought home a number of *Diemyctylus miniatus* Raf., or little red lizard or red eft, and after keeping them in a dark box filled with saturated moss, they changed their color from a bright vermilion to the olive state characteristic of the *D. viridescens*." The change took place in the autumn, and without entering the water, although they willingly remained in and under the water when placed there. He says further: "The conclusion, then, is that instead of two well-marked species or a species and a variety, we have but a single species, *Diemyctylus miniatus*."

Sarah P. Monks ('80), in discussing the differences in opinion concerning these two forms, adds: "I have also observed this change several times,"—*i. e.*, the change from the red to the viridescent form. "I have kept them (the larvæ) till they became terrestrial, and had yellow spots along their olive-green sides; but

they would not eat, and died in about a week. I am very sorry not to have been able to keep any till they reached the red eft stage. Their dying so young makes a break in the chain of observed facts that prove the red eft to be a young form of the spotted salamander. I believe, but am not able to prove at present, that the young *Diemyctylus viridescens* attains its red garb the summer it is hatched, remains that color about a year, then gradually becomes duller as it attains full size."

In 1886 Col. Nicolas Pike ('86) verified the observation that the red ones transform into the viridescent form under certain circumstances, and seems inclined to the belief of Hallowell ('56) and Cope ('59) that changed conditions produce the change in coloration: "I have gradually come to the conclusion that the two are identical. Some years ago I captured quite a number of red ones in the Catskill Mountains, brought them home and kept them in a box with other salamanders where they could resort to water if they chose. For some days they remained hiding under wet moss and stones, but finally crept out at night and went into the water. . . . In about three months they lost their bright red, and in less than a year they were of the usual olive of the *viridescens*. Another fact, still more decidedly bearing on the case, is that some two-year-old *viridescens* taken from the ponds and put in earth and dead wet leaves in a tub in my garden, without water, in a month or so began to lose their green tint and assume a dingy brownish hue. . . . When the young leave the water the food changes to spiders, insects, earthworms, etc., so totally different from the prey of the ponds, and it is most probable that this is the first cause in the change of color in the little *Diemyctylus*."

In 1890 Gage and Norris ('90) kept a bright red *Diemyctylus*, found in the woods, over the winter in a box of leaves and rotten wood with other salamanders. It was of the usual red color in the spring; but when opportunity was offered, it entered the water, and within two weeks had assumed all the characteristics of the viridescent form.

Finally, in the "Batrachia of North America" Prof. Cope thus summarizes the state of knowledge, as it then existed, with refer-

ence to these two forms: "There are two forms of this subspecies, which have received the names of *viridescens* and *miniatus* respectively. These have been shown to be stages of one and the same animal; they are not distinguished otherwise than as seasonal forms, which may be by reason of the environment rendered permanent for a longer or shorter time" (p. 207).

As seen by the above quotations, Say apparently made but a single species of the red and viridescent forms; but some later authors even placed them in different genera. Their great similarity was, however, remarked upon by Storer and others. Finally, since the work of Baird in 1850 they have remained in the same genus, but have been by many considered as distinct species. A further study and more careful observation of living specimens, have, since 1850, indicated the probability, and finally showed the certainty, that the two forms were states of the same species ('56-'90). Furthermore, these observations not only showed that the red, terrestrial form changes to the viridescent, aquatic form, but, where the matter is discussed, it is assumed that the reverse may occur, the difference of coloration, roughness, etc., being dependent upon season, food, and environment (Hallowell, '56; Cope, '59, '87; Pike, '86).

While Say ('19) says the young is of a uniform orange color, the sentence immediately following that statement, "It is decidedly aquatic," leaves one in doubt concerning his actual knowledge concerning the two forms. There is one author, however (Monks, '80), who distinctly intimates, although unable to prove, that the red form is a stage in the development of the *Diemyctylus*. Both Say and Monks are silent concerning the possibility of a return of the viridescent to the red coloration.

In order to complete the chain in the life-history of the *Diemyctylus*, and to determine so far as possible its habits, structure, physiology, and transformations during the varying phases of aquatic and terrestrial existence, the writer has availed himself of every opportunity for investigating it during the last six years. The results of this study may, perhaps, best be given by commencing with the egg:

Fertilization and Ovulation.—It has been assumed by most observers that, in analogy with the European tritons, the eggs of *Diemyctylus* are internally fertilized (Baird, '51; Whitman, '85). It is said to be external by Col. Pike ('86), who supposed that the eggs were laid in masses. So far as I have been able to ascertain, no one has previously undertaken experiments to definitely settle this point. The mode of copulation, if it may be so called, is so different from that described for the European tritons in which internal fertilization has been demonstrated that from it alone one would not expect internal fertilization. The hind legs of the male are exceedingly strong, and have developed on the ends of the toes dark, horny masses, also horny ridges along the inner or opposed surfaces of the legs (Pl. XXIII., Fig. 9). These are mostly absent in the summer. As the animals slowly move about in the water, when the male comes sufficiently near a gravid female, there is a rapid movement of the body to get above her, then the two powerful legs come together like the jaws of a steel trap, grasping the female either just in front or just behind her front legs. The ventral side of the male is thus applied to the dorsal side of the female in the thoracic region, and consequently the cloacal openings are very widely separated. The male keeps his position for an hour or longer, and during part of this time, as Baird ('51) remarks, "jerks the female round in the water most unmercifully." The cloaca of the male is very widely open and pressed against the back of the female, and when not swimming around the tail is waved from side to side. The cloacal papillæ or villi are brought into view by the eversion of the cloaca. They remind one of the cloacal villi or of the gill filaments of a male *Necturus*. In case the female shakes the male off, as sometimes happens, the cloaca of the male may remain everted, and the tail is waved from side to side while resting on the bottom or on a branch of vegetation. This also occurs when he voluntarily leaves her for the purpose of depositing spermatophores (Zeller, '90; Jordan, '91).

As the egg-laying never takes place during the mating, the eggs must be fertilized after laying by the zoosperms diffused in the water, or the zoosperms must in some way get into the cloaca or

oviduct and fertilize the eggs before they are laid. To determine which of these alternatives was correct a clean jar, holding about two liters of water, was taken, and in the water was placed a pair of *Diemyctylus*. About half an hour after the mating had ceased the water was filtered through absorbent cotton. Adhering to the upper part of the filter were multitudes of zoosperms. This showed that the zoosperms were emitted into the water. Another clean jar was then taken and partly filled with water from the university water supply, and into it were placed some *Anacharis* and *Ceratophyllum* that had been in the laboratory all winter, and not in contact with *Diemyctylus*. The female was then carefully rinsed in several waters, and finally under the tap, to ensure the removal of zoosperms from the surface. She was then put into the clean jar with the water plants. It was believed that in this way external fertilization would be precluded, and that if eggs were laid and developed it would prove internal fertilization. Commencing the day after isolation, this female laid eight eggs in four days (from the 9th to the 13th of April).

In laying the eggs the female would select a place, usually a well-leaved part of the *Anacharis* or *Ceratophyllum*. This was then clasped by the hind legs, and held close to the cloacal prominence. The body showed several writhing or serpentine movements, the legs were pressed somewhat more closely together, and then the female would move away without looking around to see whether or not the egg was securely protected. When first laid the albumen is quite cloudy, but soon clears up; it is also very adhesive, so that when forced in between the leaves it sticks to them and holds them together. It usually took from five to ten minutes to lay an egg. Those observed were laid in the daytime.

In case no green vegetation is present, the eggs are laid on bare stems (Pl. XXIII., Fig. 1) or on stones. The eggs must be laid on stones in nature when no vegetation is present, as occurs in some parts of Cayuga Lake, where they were found mating.

After a few days all but two of the eggs showed signs of development, and embryos in various stages were secured and sec-

tioned. Some were allowed to go on till hatched. This occurred in thirty-three days after the eggs were laid.

After laying the eight eggs no more were laid for over a week. She was then placed with a male for two or three days, when mating again occurred. After mating, she was again isolated as before to see if the ovulation would recommence, and if the eggs would be fertile. Seven days after isolation she commenced to lay eggs, and continued to do so until six or seven were laid. These proved fertile, and several stages of development obtained. This experiment indicates that for a single mating about six eggs may be internally fertilized, about the number found in the two oviducts at one time. It indicates, further, that in nature more than one mating probably occurs (see below); and finally, almost certain proof is given that the eggs are not externally fertilized, as in the last experiment none were laid until seven days after isolation. Three other females were isolated as described above, and the eggs proved fertile.

From these experiments it appears almost certain that the ova are internally fertilized, and as to the way in which the zoosperms reach the eggs, as there is no approach to a true copulation, the explanation of Professor Baird ('51) must be the correct one: "The seminal matter becomes diffused in the water, and fecundates the ova while still in the lower part of the oviduct." Or more probably the spermatophores recently described by Zeller ('90) and Jordan ('91) in some way aid the entrance of the zoosperms more surely than would simple diffusion in the water.

The time of ovulation was found to begin the first week in April in specimens obtained from a spring-fed pond, and to continue in different specimens from this pond till after the first of May. In specimens from Cayuga Lake, June 13th, eggs were obtained until June 18th. Probably in specimens obtained later eggs might have been obtained also. It would appear from this that the ovulating season is much earlier in the inland ponds than in the lake.

Autumnal Mating.—If adult specimens are obtained from their natural habitat in the autumn, the males will be found to possess the dark horny toe-tips and the ridges on the thighs as shown in

Pl. XXIII., Fig. 9; and the tail-fin will be found as fully developed as in April. It has also the wavy appearance as if it were too long for the tail. If the two sexes are placed together a typical mating will occur, and the emission of spermatophores will occur exactly as described for the spring, or proper breeding season (Jordan, '91). Observing the act of emitting the spermatophore and its subsequent examination is greatly facilitated by using a clean glass jar containing very little vegetation. The spermatophore is anchored on the bottom of the glass jar, and has the general appearance of a drinking-goblet,—that is, the attached part is like the broad base of the goblet,—and this is continued into a narrow part, upon the summit of which the oblong sperm-mass or sperm-ball (about 2x4 mm.) is attached, thus occupying the position of the cup part of the goblet, to continue the comparison. At first the sperm-mass is detached from the spermatophore with some difficulty, but later much more easily. If it is transferred to a watch-glass or a slide and examined in water, using preferably dark-ground illumination, the sperm-mass will appear like a mass of white ringlets, there being hundreds of zoosperms in each ringlet. The motion of the zoosperm as a whole, and the active waving of the lateral membrane or frill, is very vigorous. It was found also that isolated males would emit spermatophores, thus making them comparable with the European Triton (Gascoe, '80).

It is not easy to understand the purpose of this autumnal mating, as no eggs were ever found in the oviducts in the autumn, and it is not known that ovulation takes place at other times than in the spring, or breeding season proper. Judging from what has been found concerning European forms, where the eggs laid proved fertile although wintered in the aquarium, and not in contact with the male since its capture, also from the several broods of young from the *Salamanda atra* with but a single fertilization, it appears probable that the zoosperms are stored in some way by the female until the time of ovulation. (See Gascoe, '80; Fatio, '72; Jordan, '91; Czermak, '43; V. Siebold, '58; Zeller, '90.)

So far as I know, the presence of the horny toe-tips and thigh ridges and the prominent tail-fin have been uniformly described

as characteristic of the spring,—that is, the breeding season proper. So also the autumnal mating is, so far as I know, an entirely new observation. It was observed many times by myself, and at two different times independently by Mr. F. B. Maxwell, fellow in zoology and botany in Cornell University.

Habits of the Larvæ and Duration of the Larval Period.—The eggs of the *Diemyctylus* hatch in from twenty to thirty-five days, depending upon the temperature. From the first the coloration approaches that of the viridescent form; it has also the slim appearance and delicate outlines of the more mature ones. The gills are very prominent at a very early age, and project obliquely over the back. The larvæ are very timid and exceedingly active when they move. Frequently they remain for a considerable time in the clear water of the aquarium, with the beautiful red gills outspread and the body straight as an arrow. If disturbed in any way they dart into the vegetation like a flash. The body is narrow and the head pointed, thus forming a very marked contrast with the broad-headed *Amblystoma* larvæ. Indeed, they so strikingly resemble the adult viridescent form that it is not difficult to recognize them.

When several different kinds of larvæ are in the same aquarium, they differ from the adult aquatic form, however, in that the tail-fin extends almost to the head as a dorsal crest, something as in *Triton cristatus*.

The food appears to be entirely of an animal nature. Specimens from the ponds where the conditions are entirely normal contained minute Crustacea, larval insects and snails, and in some, aquatic worms were found. The larvæ in the aquarium were kept in food by an occasional addition of water and vegetation from their natural habitat. Early in August, while the gills are still prominent, the characteristic vermilion spots commence to appear, thus giving the larvæ a still more striking resemblance to the adult (Pl. XXIII., Fig. 3). Water is frequently taken into the mouth and passed through the gill openings for respiratory purposes, and the oral epithelium is stratified and non-ciliated, as in *Necturus*. The œsophagus is lined with ciliated epithelium, but none is present at any time in the stomach, thus further agreeing with

Necturus and differing from the larvæ or tadpoles of the bullfrog (*Rana catesbiana*) (Gage, '85, Gage, S. H. and S. P., '90).

During the last half of August the gills begin to be absorbed and also the tail fin, and the larva more frequently goes to the surface for air. Finally, during the last of August and the first of September, the gills and tail fin being nearly absorbed, the larva keeps its head out of the water an hour at a time, and finally crawls out of the water entirely.

The larvæ do not, apparently, all transform during the first summer, for specimens with gills have been taken from upland ponds in November. The size attained by the larvæ before transforming is quite various. Those observed by me were usually about the size shown in the plate (3 to 4 centimeters long); but they may become much larger. Indeed, they may remain in the branchiate condition till they are as long as some of the adult aquatic ones, and two or three times the length of some of the red ones found in nature. Large branchiate larvæ were obtained for me by Instructor Pierre A. Fish from a fresh-water pond at Wood's Holl, Mass. The tail-fin is small in these large larvæ, and there is no crest extending to the head as in the smaller larvæ. Other unusually large-gilled larvæ will be described by Prof. O. P. Hay in the forthcoming report on "The Batrachians and Reptiles of Indiana," soon to appear in the report of the Geological Survey of Indiana.

Terrestrial Life.—In order to keep the young newts alive and in health, a large glass dish was taken and a considerable amount of moist leaves and rotten wood put into it. This was an attempt to imitate nature as nearly as possible. The young newts did well, and gradually began to assume a reddish brown color on the back instead of the viridescent color (Pl. XXIII., Fig. 4). The belly became orange. In fact, it was passing through an almost exact reversal of the transformation of a red into a viridescent form. Late in September and during the first half of October the appearance was that of a rather dark "red newt." Specimens of the same size found in nature at about the same date showed the transformation of the coloration even more strikingly, as it was of a lighter red over the whole body.

During the transformation from the gilled aquatic to the gill-less terrestrial state the gill slits grow up, and the stratified, non-ciliated, oral epithelium of the aquatic larva is changed for a ciliated epithelium. The vermilion spots have one or more black pigment blotches bordering them, but there is rarely, if ever, a complete black ring around them as in the larger specimens (Pl. XXIII., Fig. 5). The spots differ in size, shape, and somewhat in arrangement in different specimens; in some the number on the two sides is different (Pl. XXIII., Figs. 4, 8). The general coloration of the body is almost always lighter on the ventral than on the dorsal portion, and differs greatly in different specimens. In some specimens it is a bright color in which the yellow is very prominent, in others the shade is more red, and in still others it is a dingy reddish brown. As shown in Fig. 7, the area of deeper dorsal red corresponds closely with the area that becomes viridescent in the adult form. As to the seat of the coloration, it is mostly due to the network of branched cells under the epidermis. The cells of the epidermis at the opening of the cutaneous glands—*i. e.*, at the summits of the papillæ or tubercles—sometimes become brownish, and in specimens that have not moulted for some time give a dingy look.

It is a curious fact that in these red forms and in the adult green ones the so-called fat-body is almost invariably of the color of the skin on the ventral portion of the body, and under the microscope shows reddish bodies almost exactly the color of the coloring matter in the chromatophores under the epidermis. The vermilion spots are produced by a deeper or redder coloration of the chromatophores. With the micro-spectroscope no distinctive absorption bands were found.

The food during the terrestrial life consisted of spiders, insects and insect larvæ, and earthworms. The larger red specimens in captivity take earthworms with great readiness. In nature the red ones live in situations, mostly at a considerable distance from water, and as well remarked by Baird ('51), is the most terrestrial of all the American salamanders. It is found under sticks and stones, and especially under rotten logs and in moist woods. It is

very rarely seen wandering around except after a rain, hence it is quite generally believed by non-naturalists to rain down.

Their movements are quite rapid, and very quickly disappear if placed where they can crawl into the grass or among leaves. They will overcome quite prominent obstacles, and in getting down from a considerable height they use the tail as a fifth hand, like a monkey, and can practically support themselves nearly their whole length. The aquatic form also frequently makes use of the tail as a kind of hand in making its way around in the submerged plants. Sometimes they give out a kind of shrill squeak or cry, but this is not very frequent. The adult aquatic ones occasionally emit a similar cry also.

Although I have been unable to keep them in confinement from the egg until their final transformation into the adult viridescent form, I have been able to obtain from a locality where they were especially abundant¹ such a complete series that it is believed that the terrestrial life continues until the autumn of the third or the spring of the fourth year after hatching,—that is, when they are two-and-a-half or three years old.

Transformation into the Adult.—As previously stated, this transformation may take place either in the autumn or the spring, and in either of these times the transformation may take place: (1) while still on dry land; (2) after entering the water.

1. As the red *Diemyctylus* attains maturity (judging from the generative organs) it gradually assumes a brownish tint, which merges slowly into a viridescent coloration of greater or less intensity in different specimens. This may occur in the autumn without entering the water, but if placed in the water it willingly remains (Kelly, '78). In two specimens under my own observation, kept in a jar containing moist rotten wood, leaves, etc., the change came about the middle of September. One was of an especially brilliant red, but within two weeks

¹ The favorable place mentioned above is Worcester, Otsego Co., N. Y., along one of the headwaters of the Susquehanna River. The specimens were obtained for me by my nephew, Albert Gage. About 12 miles from Ithaca the red form is also exceedingly abundant in and near an upland forest. This forest is not far from marshy places which are sources of small tributaries to the Susquehanna River on the south and Cayuga Lake on the north.

it, as well as its less brilliant companion, had assumed the characteristic coloration of the viridescent form. These two specimens were fed earthworms occasionally and kept in the jar until the following July. There was not the slightest indication during this period of nearly a year of a return to the red coloration, and the epithelium of the mouth remained ciliated. In the middle of July they were placed where they could enter the water, which they did with great readiness, and remained under for a considerable time at first. The time under water increased in length until within two or three days the pharyngeal respiration under water was fully established; and if put with specimens from pond or lake they could not be distinguished either by appearance or behavior. Furthermore, viridescent specimens from the water have been kept in the air for several months, but there was never any indication of a return to the red garb of the immature form. It was found, as shown in the accompanying plate, that some specimens from the water inclined to a brownish green, hence it was found desirable to note carefully the appearance at the beginning of the experiments. These experiments and observations seem to the writer to entirely preclude the notion that the red form owes its coloration to either food, season, or situation; but that it is normal for a given stage of its growth and development. It is believed also that this change of the red to the viridescent form without entering the water accounts for the belief among some naturalists that the adult aquatic forms voluntarily leave the water and become terrestrial.

2. In the observations of Col. Pike ('86) the transformation from the red to the viridescent form took place after entering the water, and apparently took place in the summer or autumn, although he does not state distinctly. In the cases observed by me one specimen was kept over winter in wood humus, and in the spring given opportunity to enter the water. It did so in a short time, and within two weeks had completely transformed. Two other specimens were found in the woods in the early spring; they likewise entered the water after a few days and gradually changed their red for the iridescent coloration, and assumed an aquatic life with the accompanying pharyngeal respiration and

non-ciliated oral epithelium. Observations have not yet been sufficiently numerous or under sufficiently normal conditions to determine how soon after becoming viridescent and entering the water eggs are laid.

Adult.—By the adult is here meant the olive-green or viridescent form (Pl. XXIII., Figs. 8–11). The normal habitat of the adult *Diemyctylus* is the water. In Ithaca, N. Y., Cayuga Lake, permanent pools in marshes and permanent spring-fed ponds in the higher or upland are favorite homes. The streams running into the lake are liable to sudden freshets, and *Diemyctylus* is rarely found in them, at least not within a mile or two of the lake valley. Specimens have been taken from the spring-fed ponds at all times of year except the depth of winter. For catching *Diemyctylus* in situations where the vegetation is abundant the best method has been found to take a strong net with a long handle and make blind sweeps with it in the water. Frequently where there is no sign of animal life, *Diemyctylus* and other batrachians may be taken in considerable numbers in this way. According to Storer and Holbrook, they may be seen occasionally in winter, swimming with great vigor under ice an inch thick. It is believed from the preceding that after once assuming an aquatic life the adult never leaves the water except on the drying of the ponds or a special scarcity of food. It is further believed from the facts stated above that although the aquatic forms may be kept in moist places out of the water for months, they never revert to a red coloration, and also that the viridescent forms found on land are in the great majority of cases transformed red ones that have not yet entered the water.

The food consists of insect larvæ, like caddis worms, adult insects, various aquatic worms, earthworms, small Crustacea, bivalve, and univalve mollusks. In captivity they learn to take bits of meat from a stick, to catch flies thrown on the water, and to catch tadpoles. It is quite possible that they indulge in this last mark of affection to their relatives in nature also. When catching tadpoles or other living prey the process is something as follows: The *Diemyctylus* moves slowly within reach of the prey, and remains perfectly quiet until the prey moves, when it is

snapped up quick as a wink, and it is rare that a failure is made. A tadpole is also liable to be caught if it attempts to swim by the *Diemyctylus*. In taking earthworms on land there is an attitude of the body and curve of the neck strikingly like the restorations of some of the ancient saurians seen in works on paleontology.

Moulting.—Both the red and the viridescent forms shed the skin at various times throughout the year. There seems to be no regular time, as in June, mentioned by some authors. In the terrestrial form the exuvium is liable to be much torn, but frequently I have seen in Cayuga Lake perfect specimens floating in the water, and appearing, as one might imagine, like the ghosts of their former owners. I have never seen the cast skin rolled up and swallowed by the aquatic form; but the terrestrial ones pull the exuvium off the tail with the mouth and afterwards swallow it.

Respiration and Relations to Oral Epithelium.—In the beginning of larval life the respiration is wholly aquatic; then, as the lungs become developed, it gradually changes to a mixed or combined respiration,—*i. e.*, to a respiration partly aërial and partly aquatic. Later, when the larva leaves the water and becomes terrestrial, the respiration becomes wholly aërial. Upon transforming to the viridescent form, and reëntering the water, the respiration again becomes mixed.

If one observes a terrestrial *Diemyctylus* carefully the floor of the mouth and pharynx will be seen to sink and rise alternately, and many times per minute. The appearance in pharyngeal inspiration may be seen in Fig. 10; in expiration, in Figs. 7 and 11. The same pharyngeal movements may be seen in a frog or turtle. On entering the water the *Diemyctylus* remains under for a considerable time, and during its submergence the same rhythmical pharyngeal movements occur, and water instead of air is alternately taken into the mouth and expelled, as in the soft-shelled turtles; and, as in the soft-shelled turtles, it is believed that it is for respiratory purposes (Gage, S. H. and S. P., '85). It is further believed, from chemical analyses, and from experiments made with the respiration of tadpoles and with Ganoid fishes, that whenever respiration is thus mixed or combined "the aërial part

is principally to furnish oxygen and the aquatic part to eliminate carbon dioxide" (Wilder, '77; Gage, S. H. and S. P., '85, '86, '88; Mark, '90).

It has been found in every one of a great many cases that whenever the respiration is wholly aërial, the entire mouth cavity is lined with ciliated epithelium which is directly continuous with the ciliated epithelium of the œsophagus. This is found not only in the red forms and the viridescent forms that had not yet entered the water, but when an aquatic form was kept in the air for ten days or two weeks the epithelium of the mouth was likewise found to be ciliated like that of the proper aërial forms. This was verified on several specimens and direct comparisons made with specimens from the same aquarium.

The branchiate larvæ and the adult aquatic forms have an oral epithelium of non-ciliated cells, as in *Necturus* and *Cryptobranchus*. It is astonishing to see how quickly a *Diemyctylus* with purely aërial respiration and ciliated oral epithelium will assume a partially aquatic or mixed respiration and the ciliated epithelium of the mouth become non-ciliated. The change has something of the character and certainty of a simple chemical reaction, and appears to show the direct relation of the mode of respiration to the character of the oral epithelium.²

² To determine whether or not the mouth has a lining of ciliated epithelium, the animal is pithed and the slit of the mouth is continued along the body beyond the stomach. The floor of the mouth is turned over and the œsophagus slit into the stomach. In this way the mucosa from the tip of the snout to and into the stomach is freely exposed. Then minute blood-clots—a method first devised by Mrs. Gage, so far as I know—are placed on the mucosa at various points. Care is taken that there shall be no drying of the membrane by keeping it well moistened with blood serum or spittle. In this way it is exceedingly easy to determine whether or not there is a complete lining of ciliated epithelium, for the ciliary currents quickly sweep the blood-clots toward and finally into the stomach. It is also an excellent method for discovering small ciliated areas. In addition to this, careful microscopic examinations were made of the epithelium from various parts of the mouth. This, of course, had to be the method employed in determining the character of the oral epithelium at the beginning of an experiment with living specimens. In the scrapings from the mouth of an aquatic *Diemyctylus* a few ciliated cells may be found under the microscope, but in such specimens there were no demonstrable ciliary currents. The source of the few cells is thought to be from the opening of the glottis or from the ciliated lining of the mouths of the buccal glands.

Conclusions.—So far as I have yet been able to learn from the opinions of others or my own observations, no explanation has offered itself for the bright color of the terrestrial, red form. The color renders it exceedingly conspicuous, and there is no counterbalancing compensation in sexual selection, for the red form is sexually immature. The olive-green or viridescent color of the adult does render it inconspicuous in green terrestrial or aquatic vegetation; they are sometimes found in large numbers in water nearly devoid of vegetation, however.

With reference to the change from the aquatic to the terrestrial life, and later the return to an aquatic life, there is perhaps a more satisfactory explanation or hint. *Diemyctylus* conforms in habits with the vast majority of batrachians in going to the water to lay its eggs. Still conforming to the habits of the group, the larvæ, on reaching a certain stage of development, absorb their gills, leave the water, and become air-breathers. It is not the purpose of this paper to attempt a discussion of the causes which led, in the course of evolution, to the assumption of an aerial for an aquatic existence by the *Diemyctylus* and many other Batrachia. It must be assumed that the reasons were sufficiently potent. Two will occur to every one conversant with the breeding places of the batrachians,—the danger of the drying of the water, and the limited amount of food.

With but few exceptions, the preparation for reproduction requires the terrestrial forms to again enter the water, and the life becomes for a greater or less time once more partially aquatic. A partial return to an aquatic mode of respiration, and the taking in of water by the pharyngeal movements described above, is by no means restricted to *Diemyctylus*, but it may be seen in such highly terrestrial forms as the little brown tree-toad (*Hyla pickeringii*) and the yellow-spotted salamander (*Amblystoma punctatum*). It appears as if the surroundings of larval life, and the necessity for respiration brought about by the prolonged stay under water required for fertilization and ovulation recalled by a kind of organic memory the mode by which respiration was accomplished in larval life.

In *Diemyctylus* this mixed respiration and the food supply apparently proved so satisfactory that the aquatic life again became fixed, and, acting through numberless generations, the tendency to revert to aquatic life became so great that maturing forms sometimes enter the water at least six months before the breeding season (Kelly, '78). It does not, however, revert so completely to an aquatic life that it cannot, in case of necessity, again become terrestrial for a considerable time.

This permanent reversion to a primitive mode of life by *Diemyctylus* does not stand alone among the Batrachia. It is paralleled and even exceeded by *Siren*, which after passing through the ordinary larval metamorphosis, has its gills so far absorbed as to be mere stubs. It then not only returns to the water, but actually reacquires its gills (Cope, '85). These two cases seem to point to the conclusion that in the course of evolution the dangers and hardships of the land became equal or greater than those of the water for these forms, and they, by readjusting themselves to an aquatic life, rendered the struggle for existence less severe. Certainly there is no reason, in the fundamental idea of evolution, why an animal may not revert to an earlier condition, provided it becomes as markedly to its advantage as was the original departure from that condition.

Summary.—1. The red and the viridescent forms of *Diemyctylus* belong to the same species, the red form being an immature condition.

2. The ova of *Diemyctylus* are internally fertilized, and are laid singly on a submerged leaf, or between submerged leaves, and partly concealed by folding the leaves closely together. If no leaves are available, the eggs are laid on stones or bare stems. The eggs hatch in about thirty days.

3. In from three to four months after hatching, vermilion spots appear, and are symmetrically arranged along the dorsal aspect next the head. The general appearance is then strikingly like that of the adult male in the breeding season, except that the tail crest, instead of ending opposite the pelvis, extends nearly or quite to the head, as in the crested Triton. Later, gills and tail-fin atrophy, and the respiration becomes more and more aerial.

4. After the gills are absorbed the animal leaves the water, and the color gradually changes from an olive-green to brownish-red, and finally, during the same season, assumes a bright yellowish-red, the vermilion spots remaining and becoming partly surrounded by black pigment.

5. As the terrestrial life is assumed the stratified, non-ciliated oral epithelium of the aquatic larva gradually changes to a ciliated epithelium continuous with that of the œsophagus.

6. In the autumn of the third or the spring of the fourth year after hatching (when two and one-half or three years old), the red changes for a viridescent coloration. This may occur with or without entering the water. If the water is entered the animal changes to an aquatic mode of life.

7. On reassuming an aquatic life the ciliated, oral epithelium becomes again stratified and non-ciliated, as in the aquatic larva, and as in *Necturus* and *Cryptobranchus*.

8. After becoming adult and transforming to the viridescent coloration, the *Diemyctylus* always remains of that general color, and never again becomes red, even when kept out of water a whole year, thus showing that the coloration is dependent neither on food, season, nor environment, but is normal for a given period of life only.

9. The adult viridescent forms are purely aquatic under favorable conditions, and after once entering the water do not leave it, although they are able to live for several months, and perhaps indefinitely in moist places, wholly out of water. Rhythmical pharyngeal respiration is very marked both in air and under water.

10. The character of the oral epithelium seems directly dependent on the mode of respiration, being stratified and non-ciliated with a purely aquatic or a mixed respiration, and ciliated with a purely aërial respiration.

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EXPLANATION OF PLATE. (FRONTISPIECE.)

Transformation of *Diemyctylus viridescens*. Drawn from photographs and colored from nature by Mrs. Gage. All are natural size, except Fig. 2 and the vermilion spot, Fig. 5.

FIG. 1.—Branch of *Ceratophyllum* with *Diemyctylus* eggs between the needle-like divisions of the leaves; also nearly bare stem of *Anacharis* with egg attached.

FIG. 2.—*Diemyctylus* egg, in the yolk-plug stage of development, attached to an *Anacharis* leaf. It was from an isolated female, and the parchment-like envelope is ovoid. Outlined with an Abbé camera lucida, and magnified about seven diameters.

FIG. 3.—Dorsal, ventral, and lateral views of a larval *Diemyctylus* in August and September. The gills are considerably atrophied, and the coloration and vermilion spots resemble the adult.

FIG. 4.—Dorsal and ventral view of a larval *Diemyctylus* the last of September and first of October, after it has become entirely terrestrial and was gradually assuming a bright red color.

FIG. 5.—Enlarged vermilion spot with complete black ring.

FIG. 6.—Ventral view of a red *Diemyctylus* taken in the spring, and either two or three years old. This light yellowish-red color is very common. The enlarged vermilion spot (Fig. 5) is to show that in animals of this size and in the adult the vermilion spots are usually entirely surrounded by a black pigment ring.

FIG. 7.—Lateral view of a red *Diemyctylus*, to show the difference in coloration of the dorsal and ventral portions of the body. By comparing with the viridescent forms it will be seen that the deeper coloration corresponds in situation in the two. The darker red shown in this figure is perhaps more common than the color in Fig. 6.

FIGS. 8, 9, and 10.—Views of an adult male *Diemyctylus* in October. It was in this specimen that pharyngeal respiration under water was first noticed, in 1886. The color varies considerably, some being darker and some lighter than here shown.

FIG. 8.—Dorsal view. The number of vermilion spots is seen to be few and to differ on the two sides. As shown by the different figures on this plate, the number of vermilion spots varies considerably.

FIG. 9.—Ventral view, showing the dark, horny thickenings on the tips of the toes, and the ridges (commonly six) on the inner or opposing surfaces of the legs. These horny developments mostly disappear during the summer, immediately after the breeding season, and reappear in the autumn.

FIG. 10.—Lateral view, showing the tail-crest or fin, extending on the dorsal side to about opposite the pelvis,—not to the head, as in the European Tritons. This fin is less marked in the female (see Fig. 12), and partly disappears after the breeding season. The cloaca is partly everted, and shows some of the lining fringes or villi. The floor of the mouth and pharynx are depressed as when filled with water or air in pharyngeal respiration. Compare Fig. 11.

FIG. 11.—Lateral aspect of a gravid female. This coloration is frequent in adult forms found in water. The hind legs and the tail fin are smaller than in the male. The pharynx and floor of the mouth are raised as in expiration,—*i. e.*, when the air or water is entirely expelled.